Taxonomy, Mature Larva, and Observations on the Biology of *Gnamptopelta obsidianator* (Brullé) (Hymenoptera: Ichneumonidae, Ichneumoninae)

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Abstract.—The two nominal species in *Gnamptopelta*, *G. obsidianator* (Brullé) and **G. austrina (Cresson)**, do not merit separate species or subspecies status, and the latter is synonymized under the former; the genus is hence monotypic. Specimens reared from *Amphion floridensis* (B.P. Clark) (Lepidoptera: Sphingidae), probably attacked in captivity, represent the first verified host record for *Gnamptopelta*. A description of the mature larval exuviae is provided. Observations of the wasps in the field and in captivity suggest that *G. obsidianator* directs its host-searching to grape-vines (*Vitis* spp.), and that its host range may not include all grapeleaf-feeding sphingids.

Gnamptopelta obsidianator (Brullé) is one of the largest ichneumonids in eastern North America and one of the most striking, with its black body, yellow antennae, and, in some southern populations, extensive reddish coloring of the head and anterior mesosoma. While it is commonly collected on the wing and is well represented in collections, no credible hosts have previously been reported. The genus is currently placed in the Trogini, subtribe Callajoppina; nearly all recorded callajoppine hosts are Sphingidae (Heinrich 1962). Heinrich (1977) noted that *G. obsidianator* frequents grapevines (Vitaceae: *Vitis* spp.), which are the food plants for at least 10 sphingids in North America (Forbes 1948; Hodges 1971). Thus, guided by taxonomic inference and a few incidental observations, we set out to identify the hosts of *G. obsidianator* by rearing *Vitis*-feeding sphingids.

We also decided to use this opportunity to clarify the status of species within *Gnamptopelta* Hopper, in which two species, *obsidianator* (Brullé) and *austrina* (Cresson) were originally included. Subsequent authors (Townes and Townes 1951; Heinrich 1962, 1977; Carlson 1979) have considered *austrina* to be a subspecies of *obsidianator*, although Heinrich (1977) hedged that the subspecies could be "ecologically differentiated species parasitizing 2 different hosts living on the same plant."

The *Gnamptopelta* specimens examined in this study are in the American Entomological Institute (Gainesville, Florida: AEIC) and the Florida State Collection of Arthropods (Gainesville, FL: FSCA).

TAXONOMY

Heinrich (1962) placed *Gnamptopelta* in the tribe Trogini, subtribe Callajoppina, which also contains the genera *Afrotrogus, Callajoppa, Catadelphus, Conocalama, Dimaetha, Holojoppa, Pepsijoppa, Stirojoppa, Tmetogaster, Tricyphus,* and *Yeppoona* (Ward and Gauld 1987; Yu and Horstman 1997). All reliable host records indicate that these genera parasitize only Sphingidae.

Hopper (1939) erected *Gnamptopelta* for two North American species, *Trogus obsidianator* Brullé and *Trogus austrinus* Cres-

son. These were distinguished on the basis of color: *G. austrina*, found in South Carolina, Georgia, and Florida, had the head and anterior mesosoma reddish while *G. obsidianator*, found in the remaining part of eastern North America west to the Rocky Mountains, had the entire body black except for the yellowish-white paraocular area. With the exception of Townes (1944), later authors (Townes and Townes 1951; Heinrich 1962, 1977; Carlson 1979) have treated *austrina* as a subspecies of *obsidianator*. Heinrich (1962) could not decide whether the taxa represented two species or a single species with two color forms. After studying the Florida ichneumonine fauna (Heinrich 1977), he concluded that for *Gnamptopelta*: 1) "*austrina* . . . occupies the peninsula of Florida except its most northern part, and that the uniformly black *obsidianator* occupies the entire eastern territory of continental North America, including the base of Florida"; 2) "sporadically, however, *obsidianator* also occurs in the territory of *austrina*, and likewise, sporadically, *austrina* is found in the southern parts of the territory of *obsidianator*"; 3) ". . .it also must be mentioned that "intergrades" between the 2 forms have never been found" (*op. cit.*, p. 285).

Our examination of over 550 *Gnamptopelta* specimens reveals that, contrary to Heinrich's assertions, intermediates do occur and all are found in Florida. Most of these individuals are found north of Ocala, in the northern third of the state (above 29°N). Black and intermediate specimens are found throughout the flight period (mid-February through mid-November); there is no sex bias in the color forms. An interesting series of eight males was collected at the American Entomological Institute in March and April of 1986 [AEIC]. Every variation is present, from uniformly black with no reddish markings to the extreme of an entirely reddish head, reddish anterior mesosoma, and reddish postpetiole. This series alone refutes the notion of two separate entities. We there-

fore place *austrina* as a junior synonym of *obsidianator* (NEW SYNONYM), noting a particularly apt remark that summarizes the past *Gnamptopelta* literature: ". . .too much time has been wasted on trying to assemble data, much of it illusory, to maintain already proposed names for subspecies" (Franclemont 1973).

All records to date indicate that *G. obsidianator* does not occur west of the front range of the Rocky Mountains. We have, however, seen one specimen from California ("Merced Co.; Los Banos National Wildlife Refuge, 4 mi. N. Los Banos; 12-vi-1981; D. Jamieson"; FSCA). It is uniformly black and identical to specimens from the northeastern part of the range. Queries of the major California collections have not revealed any more specimens from the West Coast. At this time, we consider the specimen to be mislabeled or perhaps the result of an import to the area.

MATURE LARVA OF *GNAMPTOPELTA OBSIDIANATOR*

Materials and Terminology.—The terminology of the cephalic sclerites of the mature larva is that of Gillespie and Finlayson (1983) and Short (1978), with modifications by Wahl (1990). The epistomal suture is the lateral groove between the anterior tentorial pits (Matsuda 1965). It is present as a distinct depression in mature ichneumonid larvae. Although the area is usually unsclerotized, a continuous sclerotized band extends across it in the Anomaloninae, Ichneumoninae, Metopiinae, and Pimplini (and isolated taxa in other subfamilies). Previous ichneumonid workers have referred to this area as the "epistoma," including in it the portion of the pleurostoma above the superior pleurostomal process. This use of "epistoma" should be eschewed. We suggest the following descriptive terms: a) epistomal suture unsclerotized; b) epistomal suture partially unsclerotized, medially incomplete (as in *Cryptus albitarsis* (Cresson); Short 1978: fig. 238); c) epistomal suture
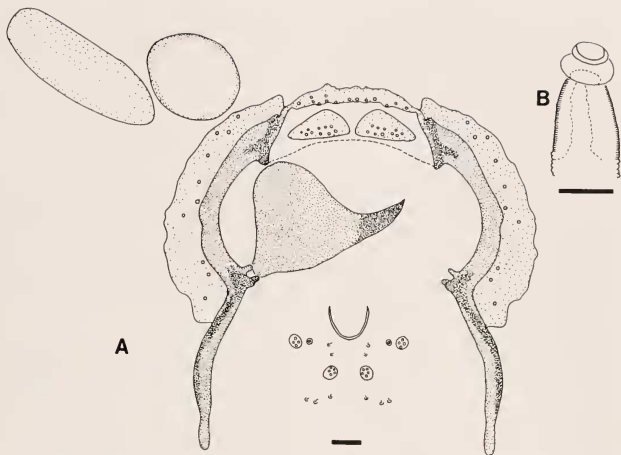
Fig. 1. Mature larva of *Gnamptopelta obsidianator*: (a) cephalic sclerites, (b) prothoracic spiracle. The scale lines represent 0.1 mm.

completely sclerotized forming an *epistomal band*.

Methods of larval preparation are those of Wahl (1989). Wahl's notation for larval preparations follows the museum acronym. It consists of his initials, the day, month, year, and a letter designating the individual preparation.

Description.—Epistomal band present, with 14 pores. Labral sclerite, hypostomal spur, stipital sclerite, labial sclerite, and prelabial sclerite, absent. Clypeolabral plates present and triangular in outline, not connected to epistomal band, and not joined or touching medially. Pleurostoma and hypostoma strongly sclerotized. Accessory pleurostomal area moderately sclerotized. Hypostoma straight, posterior end not elongate or upcurved. Accessory reticulate sclerotization prominent. Maxillary palpus with four sensilla and an adjacent sclerotized seta; labial palpus with

five sensilla and four adjacent setae. Mandible strongly and uniformly sclerotized; blade about 0.4× as long as mandible, without denticles. Antenna disc-like, rim moderately sclerotized; central papillus absent. Parietal band present and weakly sclerotized. Prothoracic spiracle as in fig. 1b: atrium with width about 0.7× as long as closing apparatus and interior with numerous long heavy spines; atrial opening with conspicuous rim; closing apparatus adjacent to atrium. Skin smooth, with widely scattered setae and without spines.

Fig. 1 illustrates the cephalic sclerites and prothoracic spiracles of the mature larva; it is a composite of two individuals collected in the Ocala National Forest (USA: Florida; Marion Co.; Lake Delancy campground area, 5.5 miles N-NW Salt Springs, 29° 25'N, 81° 47' W; K.R. Sime & D.B. Wahl; emerged 31 May 1997 [AEIC: DBW 1.vi.1997a] and emerged 19 June

1997 [AEIC: DBW 20.vi.1997a], both from *Amphion floridensis*). The characteristic absence of the labial sclerite in ichneumonines resulted in distortion of the labial region in both preparations. Consequently, placement of the salivary orifice, palpi, and associated setae is only approximate.

Discussion.—Short (1978) and Gillespie and Finlayson (1983) provide keys to final-instar larvae of ichneumonine tribes and genera. Townes and Heinrich differed regarding placement of the Callajoppina. Short follows Townes (Townes et al. 1961) in placing them in the Heresiarchini ("Ichneumonini" of Short); Finlayson accepts Heinrich's placement of these genera as the subtribe Callajoppina in the Trogini (her "Trogusini"). Both sets of keys will take *Gnamptopelta* to the correct group of genera. Further use of Short will run *Gnamptopelta* to *Callajoppa*; Gillespie and Finlayson will key it to *Conocalama*. Modification of these keys will not, in our opinion, be useful. Both are inadequate samples of the world ichneumonine fauna: of approximately 370 genera worldwide (Wahl 1993), Gillespie and Finlayson treat 25 and Short 53. Any attempted corrections of the generic keys will risk defeat when the next previously undescribed larva is found.

BIOLOGY OF *GNAMPTOPELTA OBSIDIANATOR*

Observations.—Field work was conducted in the Ocala National Forest, in north-central Florida (29° 25'N, 81° 47' W), where both grape and *G. obsidianator* are abundant in the spring (March to May). The study site is part of an extensive stand of longleaf pine (Pinaceae: *Pinus palustris* Miller), with an open understory dominated by wiregrass (Gramineae: *Aristida stricta* Micheaux) and scattered low shrubs, chiefly scrubby oaks (Fagaceae: *Quercus marilandica* Muenchhausen and *Q. laevis* Walter), and pawpaw (Annonaceae: *Asimina speciosa* Nash and *A. obovata* Willdenow). Two species of grape are

Table 1. Summary of field observations of female *obsidianator.* Identification of plants landed upon with searching times, recorded when possible, in parentheses. Before 8 April we had not confirmed the identities of *Vitis* species.

Wasp No.	Searching Sequence
1 (23 March)	*Vitis* (2-3s); *Vitis* (2-3s); *Vitis* (2-3s)
2 (23 March)	*Quercus* (<1s); *Quercus* (<1s); *Vitis* (25s); *Vitis* (lost)
3 (23 March)	*Vitis* (2-3s); *Vitis* (2-3s); *Vitis* (2-3s)
4 (23 March)	*Vitis* (2-3s); *Vitis* (2-3s); *Quercus* (2-3s)
5 (23 March)	*Vitis* (2-3); *Vitis* (2-3s); *Quercus* (2-3s)
6 (8 April)	*V. rotundifolia* (>20s); *V. aestivalis* (10s)
7 (8 April)	*V. aestivalis* (captured after 2-3s)
8 (17 April)	*V. rotundifolia* (>60s)
9 (24 April)	*V. aestivalis* (captured after 2-3s)

found here, both extremely common and often covering large expanses: *Vitis aestivalis* Micheaux and *V. rotundifolia* Micheaux. In 1997, most grape plants of both species were fully leafed out by the middle of March, and both continued to put out new leaves throughout the spring. A few *G. obsidianator* were seen as early as 10 March; the peak of abundance appeared to be during the last week of the month, when for a few days 12–15 wasps were seen each day. From then until the middle of May, when observations ceased, we usually saw 1–3 individuals in the course of 4–5 hours spent almost every day in the field.

Males fly rapidly, 2–3 meters above the ground, land rarely, and follow wide circuits in patches of forest abounding in grapevines. They were perhaps patrolling areas in which females were likely to eclose or to enter in the course of searching for hosts, although we witnessed no encounters between the sexes.

The females as well as the males are associated with grape at this field site. The females also fly quite fast, but land often. Table 1 summarizes our observations of searching behavior. Females appear to fly deliberately from one grape patch to the next, less often landing on other common low shrubs, which were usually surround-

ed by if not overlaid with grapevines. The wasps land on the upper surface of the leaf and tap it several times with the ventral surfaces of the antennae; usually, the inspection lasted just a few seconds, and the wasp then proceeded to the next plant, but in some cases the wasps stayed longer and conducted a thorough search of nearby leaves and stems. We suspect that the length of the search might be related to the presence of feeding damage or other traces left by host larvae (Vinson 1984). However, we observed no encounters with hosts in the field: the leaves searched, including those examined for just a few seconds, often bore herbivore damage, but we never found larvae in their vicinity.

Between 31 March and 2 May 1997 we collected 66 sphingid larvae on *Vitis*. We reared them in small groups (3–10 larvae) in plastic boxes which we supplied with fresh grape leaves every 1–2 days. Using Forbes's (1948) key, we were able to identify the caterpillars to species when they reached the 4th instar (and confirmed the identifications when adults emerged). All were macroglossine sphingids: *Darapsa myron* Cramer (33 reared to pupation), *Amphion floridensis* B.P. Clark (= *nessus* Cramer) (5 reared), and *Eumorpha achemon* Drury (2 reared). Larval mortality was due to braconid parasitism (*Aleiodes texensis*) killing 4th instars (10 victims, all *D. myron*) and unknown causes among 2nd-instar larvae (too small to identify). Of the *D. myron* and *A. floridensis* found during the first two weeks (about 45 larvae), all but one were small second and third instars; later collections included a few 4th and 5th instars. The two *E. achemon* larvae were found side-by-side on April 26 as very nearly mature 5th instars.

All larvae were found on *V. aestivalis*. Although we often found compelling feeding damage on *V. rotundifolia*, and this plant was inspected both by us and by *Gnamptopelta* females, we found no sphingid larvae on it: if not coincidence, this could be evidence for an oviposition pref-

erence in the adult sphingids, or for higher larval survivorship on *V. aestivalis*. Furthermore, in rearing the larvae, we found that they preferred to feed on *V. aestivalis* when both species of grape were in their boxes. This could reflect the habituation of the larvae to the plant on which they initially fed (Jermy 1987), or it could represent an inherently greater palatability of *V. aestivalis* to the larvae. As most of the larvae were *D. myron*, these observations may apply only to that species; the numbers of the other two species collected were too small for useful speculation. In addition, we noted that all larvae fed on full-sized leaves, never on the youngest leaves, which might represent an aversion to the denser pubescence of the youngest leaves (Southwood 1986) or perhaps to higher levels of allelochemicals (Feeny 1976).

The larvae of *D. myron* and *A. floridensis* have many habits that make them inconspicuous in the field. Whether feeding or resting, all instars are invariably on the undersides of the leaves, and they usually rest along the leaf veins, which the light-green young instars match particularly well in color and shape. Often the larvae rest on undamaged foliage one, two, or three leaves removed from the feeding site. The younger larvae feed in a distinctive fashion, by eating symmetrical holes on either side of the leaf, near the base, a pattern that blends extremely well with the deep rounded lobes and hollows of the leaves of *V. aestivalis*. Older larvae tend to feed along the edges of the leaf, eating off large pieces. Heinrich (1979) noted similar behaviors in the sphingid *Sphecodina abbotti* Swainson feeding on *V. vulpina* L. (in Minnesota) and suggested that this, along with the habit of staying under the leaves, conceals the caterpillars from predators that hunt by eye, particularly birds. We did not happen to observe any birds inspecting grapevines, but speculate that these behaviors may be somewhat effective against *G. obsidianator*. As the wasps

land initially on the top surface of the leaf, a caterpillar resting underneath may gain some extra time to fall off without being noticed, and its removal from the feeding site while resting might help frustrate a wasp that was initially attracted (by sight or by odor) to feeding damage (Vet and Dicke 1992).

Our observations of *G. obsidianator* and sphingid larvae in captivity suggest that letting go from the leaves is an effective means by which caterpillars elude wasps. We placed three field-caught females in a small glass aquarium (23-cm cube) with 4 larvae (at a time) feeding on grape sprigs. Some larvae (both *D. myron* and *A. floridensis*) dropped off their leaves as soon as wasps set foot on the leaves; others dropped only after the wasps' antennae or tarsi touched them. If the wasps tried to oviposit, the time it took them to bring their ovipositors into position, after making antennal contact, was long enough for the larvae to drop down and thus confound the oviposition attempt. Dropping appeared to be the main defense of smaller larvae; fourth- and fifth-instar larvae, when touched by a wasp, stayed put and swung their heads about with such violence as to parry any attempt at oviposition quite effectively, sometimes hurling the wasp against the side of the cage. The wasps, if not thrown, in many instances had so much difficulty inserting their ovipositors into the writhing caterpillars that they simply gave up.

When exploring the aquarium, the wasps tapped steadily with the extended antennae, lightly touching the apical quarter (flattened ventral surface) to the substrate. The wasps showed little interest in *D. myron* larvae, never attempting to sting them even after finding and examining them. In contrast, *A. floridensis* elicited great excitement: upon encountering a chewed leaf margin or a particle of frass, the wasps slowed their walking pace, vibrating the antennae much more rapidly and pressing them more firmly against the

surface, with more of the antennal area, approximately the apical third, making contact. Upon finding *A. floridensis* larvae, the wasps tapped them for 1–2 seconds with the antennae and then turned around to sting. We witnessed six apparent ovipositions, by two females; it appears that the eggs may be inserted anywhere into the host's body apart perhaps from the head capsule. Attempts at oviposition occurred with third-, fourth-, and fifth-instar larvae (we did not expose younger larvae).

The *G. obsidianator* that we reared came from *A. floridensis* and resulted from those larvae exposed as 3rd and 5th instars. In total, we had six *A. floridensis* larvae that grew large enough to be identified: two went to term and emerged as moths, and four others were exposed, of which one died just before and one some time after pupation and two produced the wasps. Six of the *D. myron* larvae (also 3rd, 4th, and 5th instars) were exposed to the wasps and continuously observed, but no ovipositions were attempted with these larvae and all developed into adult moths.

The sphingids, parasitized and not, pupated by forming loose cocoons amid leaves and paper towels. The adult wasps emerged by cutting off the anterior 0.1 of the host pupa. Such an emergence hole is apparently characteristic of the Callajoppina (Mell and Heinrich 1931), and appears to be the primitive condition for the Ichneumoninae (Gillespie and Finlayson 1983). The ichneumonid's rudimentary cocoon, located in the detached anterior section, consists of a cap of dark brown silk just inside the cut margin.

Conclusions.—Although it was the most common grape-feeding sphingid at our field site in spring 1997, our observations suggest that *D. myron* is not a host of *G. obsidianator*. Of 33 larvae collected on plants exposed to a considerable population of *G. obsidianator*, no wasps emerged; the wasps showed no interest in this species in captivity (and much interest in *A.*

floridensis under the same conditions). It is possible that the larvae we collected were too small for successful oviposition or were not old enough to have spent much time exposed to wasps, thus lowering the probability of parasitism, or that parasitism rates are generally very low; however, the combined field and captivity observations argue that *D. myron* is at least not a preferred host.

That *A. floridensis* is a natural host is strongly supported by our successful rearing in captivity: a koinobiont larva-pupal endoparasitoid, *G. obsidianator* is not likely to develop successfully on randomly encountered moth larvae because it must survive the immunological defenses of the host and also coordinate its development with the onset of pupation in the host (Askew and Shaw 1986; Omata 1984). *Amphion floridensis* occurs throughout the geographical range of *G. obsidianator* and is thus potentially the sole host: its range is described as extending "from Florida, north to Nova Scotia, west to Calgary, Alberta, and south to Kansas" (Hodges 1971), and our queries of various collections expand this to central Colorado and southern Texas as well. In Florida, at least, the flight period of *G. obsidianator* coincides with the larval stage of *A. floridensis* (Kimball 1965). However, we can say nothing about *E. achemon*, because we found only two specimens and did not expose them to wasps; some 10 other sphingids feeding on grape in eastern North America (Hodges 1971) also demand investigation.

Hopper (1939) lists as a host *Papilio polyxenes* Fabricius (Lepidoptera: Papilionidae), referring to a New York list for which voucher specimens are unobtainable. As may be the case for many such isolated records (Shaw 1994), this one is almost certainly specious. This swallowtail is often reared by amateurs and professionals alike, as the caterpillar is quite striking and very often found on garden herbs and common roadside weeds (Um-belliferae). We have seen scores of specimens of *Trogus pennator* Fabricius (Ichneumoninae) reared from *P. polyxenes* in collections, but no reared *G. obsidianator*; a life-history study of *P. polyxenes* in central New York State, where *G. obsidianator* is common, found that about 10% of 128 pupae were parasitized by *T. pennator*, with a few other parasitoids occurring infrequently, but no *G. obsidianator* (Feeny et al. 1985).

We conclude that *G. obsidianator* parasitizes at least one species of *Vitis*-feeding sphingid. The degree of specialization within this group is unknown, but our observations of captive wasps suggest that *G. obsidianator* does not uniformly attack available sphingid species and that it could be restricted, at least locally in Florida, to *A. floridensis*. Our results support Heinrich's (1962) contention that the genera of the *Callajoppa* group are strictly parasitoids of Sphingidae.

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LITERATURE CITED

Askew, R. R. and Shaw, M. R. 1986. Parasitoid communities: their size, structure, and development. *Insect Parasitoids* (eds J. Waage & D. J. Greathead), pp. 225–264. Academic Press, London.

Carlson, R. W. 1979. Family Ichneumonidae. *Catalog of Hymenoptera in America north of Mexico*, vol. 1 (eds K. V. Krombein, P. D. Hurd, D. R. Smith, & B. D. Burks). 1198 pp. Smithsonian Institution Press, Washington, D.C.

Feeny, P. P. 1976. Plant apparency and chemical defense. *Recent Advances in Phytochemistry, Vol. 10* (eds J. W. Wallace & R. L. Mansell), pp. 1–40. Plenum Press, New York.

Feeny, P. P., W. Blau, and P. Kareiva. 1985. Larval growth and survivorship of the black swallowtail butterfly in central New York. *Ecological Monographs* 55: 167–187.

Forbes, W. T. M. 1948. *Lepidoptera of New York and neighboring states, Part II.* Cornell University Agricultural Experiment Station, Ithaca, New York.

Franclemont, J. 1973. *The moths of America north of Mexico: Fascicle 20.1. Mimallonoidea, Mimallonidae and Bombycoidea, Apatelodidae, Bombycidae, Lasiocampidae.* E.W. Classey Ltd. & R.B.D. Publications, Inc., London.

Gillespie, D. R. and T. Finlayson. 1983. Classification of final-instar larvae of the Ichneumoninae (Hymenoptera: Ichneumonidae). *Memoirs of the Entomological Society of Canada* 124: 1–81.

Heinrich, B. 1979. Foraging strategies of caterpillars: leaf damage and possible predator avoidance strategies. *Oecologia* 42: 325–337.

Heinrich, G. H. 1962. Synopsis of the Nearctic Ichneumonidae Stenopneusticae with particular reference to the northeastern region (Hymenoptera): Part VII: Synopsis of the Trogini. *Canadian Entomologist supplement* 29: 807–860.

Heinrich, G. H. 1977. Ichneumoninae of Florida and neighboring states. *Arthropods of Florida and neighboring land areas* 9: 1–350.

Hodges, R. W. 1971. *The moths of America north of Mexico, Fascicle 21. Sphingoidea (Hawkmoths).* E.W. Classey Ltd. & R.B.D. Publications, Inc., London.

Hopper, H. P. 1939. A synoptical revision of the tribe Trogini Ashmead of the United States and Canada (Hymenoptera: Ichneumonidae). *Transactions of the American Entomological Society* LXV: 307–347.

Jermy, T. 1987. The role of experience in the host selection of phytophagous insects. *Perspectives in chemoreception and behavior* (eds R. F. Chapman, E. A. Bernays & J. G. Stoffolano, Jr.), pp. 143–157. Springer-Verlag, New York.

Kimball, C. P. 1965. The Lepidoptera of Florida: an annotated checklist. *Arthropods of Florida and neighboring land areas* 1: 1–363.

Matsuda, R. 1965. Morphology and evolution of the insect head. *Memoirs of the American Entomological Institute* 4:1–334.

Mell, R. and G. Heinrich. 1931. Zur Biologie und Systematic der südchinesischen Ichneumoninae Ashm.

(Fam. Ichneumonidae Hym.). *Zeitschrift für angewandte Entomologie* 18: 371–403.

Omata, K. 1984. Influence of the physiological condition of the host, *Papilio xuthus* L. (Lepidoptera: Papilionidae) on the development of the parasite, *Trogus mactator* Tosquinet (Hymenoptera: Ichneumonidae). *Applied Entomology and Zoology* 19: 430–435.

Shaw, M. R. 1994. Parasitoid host ranges. *Parasitoid community ecology* (eds B. A. Hawkins and W. Sheehan), pp. 111–144. Oxford University Press, Oxford.

Short, J. R. T. 1978. The final larval instars of the Ichneumonidae. *Memoirs of the American Entomological Institute* 25: 1–508.

Southwood, T. R. E. 1986. Plant surfaces and insects—an overview. *Insects and the plant surface* (eds B. Juniper & T. R. E. Southwood), pp. 1–22. Edward Arnold Ltd., London.

Townes, H. 1944. A catalogue and reclassification of the Nearctic Ichneumonidae (Hymenoptera). Part I. The subfamilies Ichneumoninae, Tryphoninae, Cryptinae, Paeogeninae and Lissonotinae. *Memoirs of the American Entomological Society* 11(1): 1–477.

Townes, H, and M. Townes. 1951. Family Ichneumonidae. *Hymenoptera of America north of Mexico—synoptic catalog* (eds C. F. W. Muesebeck, K. V. Krombein, & H. K. Townes). *Agriculture Monograph* 2: 1–1420.

Townes, H., M. Townes, and V. K. Gupta. 1961. A Catalog and Reclassification of the Indo-Australian Ichneumonidae: Tribe Trogini. *Memoirs of the American Entomological Institute* 1: 1–522.

Vet, L. E. M., and M. Dicke. 1992. Ecology of infochemical use by natural enemies in a tritrophic context. *Annual Reviews of Entomology* 37: 141–172.

Vinson, S. B. 1984. How parasitoids locate their hosts: a case of insect espionage. *Insect Communication* (ed. T. Lewis), pp. 325–348. Royal Entomological Society, London.

Wahl, D. B. 1989. Further notes on preparation of exuviae of parasitic Hymenoptera. *Entomological News* 100: 181–182.

Wahl, D. B. 1990. A review of the mature larvae of Diplazontinae, with notes on larvae of Acaenitinae and Orthocentrinae and proposal of two new subfamilies (Insects: Hymenoptera, Ichneumonidae). *Journal of Natural History* 24:27–52.

Wahl, D. B. 1993. Family Ichneumonidae. *Hymenoptera of the World: an identification guide to families* (eds H. Goulet & J. T. Huber), pp. 395–442. Canada Communications Group, Ottawa.

Ward, S. and Gauld, I. 1987. The callajoppine parasitoids of sphingids in Central America (Hymenoptera: Ichneumonidae). *Systematic Entomology* 12: 503–508.

Yu, D. S. and Horstmann, K. 1997. A catalogue of world Ichneumonidae (Hymenoptera). *Memoirs of the American Entomological Institute* 58 (1–2): 1–1558.